PHYLOGENETIC ANALYSIS OF THE EARLY TABULATE CORALS

by J. M. PANDOLFI

ABSTRACT. Phylogenetic analysis of the extinct anthozoan clade Tabulata yields new hypotheses concerning their pattern of diversification in the Ordovician. Two separate phylogenetic analyses, one based on primitive rugose corals as the outgroup (RUGSGRPS), and the other based on *Lichenaria* as the ancestral tabulate coral (LICHGRPS) yielded different phylogenies. The phylogenies generated are broadly different from previously proposed phylogenies based on possibly subjective morphological interpretations, and on biostratigraphical and/or biogeographical hypotheses alone. Character analysis based on consistency index (a measure of homoplasy of characters) yielded four suites of morphological characters: (1) suites with a high consistency index (CI) that differentiate major groups; (2) suites with a high CI that differentiate subgroups; (3) suites with a low CI that differentiate major groups and (4) suites with a low CI that differentiate subgroups. Therefore, CI does not necessarily correspond with the potential for differentiating major groups. The most useful characters in differentiating major groups of Ordovician tabulates are colony architecture, wall thickness, mural pores, microstructure, corallite shape, and coenenchyme, whereas those not particularly useful in differentiating major groups are tabulae, septa, rows of septal spines, columella, and stereozone. The phylogenetic analyses corroborate the taxonomic integrity of the presently defined Auloporida, Favositida, Halysitida, Heliolitida and most Sarcinulida and falsify the taxonomic integrity of the Chaetetida and the Lichenariida. As presently defined the Halysitida should be separated from the Heliolitida.

PERHAPS the most perplexing problems in phylogenetic reconstruction are those in which the entire taxon under study is extinct. This may be due, in part, to the reliance in such studies upon strictly hard-part morphological data, which are usually incomplete. Although study of the pattern of origination of a clade has the potential to reveal much concerning the subsequent evolutionary history of the group, relatively few cladistic studies deal solely with the patterns of character state transitions in the early diversification of extinct higher clades. Resolving phylogenetic relationships among early taxa has been a major problem in reconstructing the pattern of Cnidarian radiations. In this paper, I provide a phylogenetic analysis of the earliest representatives of the extinct subclass Tabulata (Phylum Cnidaria) in an effort to identify the pattern of character state evolution during their Ordovician radiation.

One goal of the phylogenetic analysis is to test Scrutton's (1984) phylogenetic reconstruction of the Ordovician tabulate coral genera. He utilized biogeographical, biostratigraphical and morphological information in constructing his phylogeny of the early tabulates. In his morphological analysis, he used a modified criterion of parsimony in which certain morphological characters were weighted in certain clades. The phylogenetic analysis presented here is based strictly on morphological character state transformations in which parsimony is used with no weighting of specific characters.

Two phylogenetic analyses of the same data matrix are presented. The first phylogenetic analysis utilizes the most primitive Ordovician rugose corals (Scrutton 1979; Sytova 1977; Webby 1971) as the outgroup. In addition, because *Lichenaria* has been proposed as the ancestral tabulate coral and provides the starting point for many phylogenetic reconstructions of tabulate corals (Flower 1961; Flower and Duncan 1975; Scrutton 1979, 1984), I have conducted a phylogenetic analysis in which *Lichenaria* is identified as the ancestor; that is, an analysis in which all the character states possessed by *Lichenaria* are considered primitive with respect to all the other Ordovician taxa. I present the

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results from these two analyses in the form of Adams (1972) consensus trees with the goal of providing a set of phylogenetic hypotheses.

I stress that the resultant phylogenetic trees presented here are only hypotheses. Due to the large number of taxa and characters utilized in the analyses presented below, a 'solution' based on maximum parsimony cannot be obtained with current available resources. Therefore, there is no certainty that the results presented here represent the true genealogical relationships of the earliest tabulate corals. Their strength lies in the fact that they represent a set of phylogenetic hypotheses which are based entirely on morphological information which can now be evaluated with respect to others types of information such as stratigraphy and biogeography. In addition, it is hoped that this information will be useful to specialists dealing in evolutionary, functional and homology questions in corals.

PREVIOUS STUDIES

Perhaps the two most frequently cited ancestral taxa for Tabulata are *Aulopora* and *Lichenaria*. Sokolov (1962) suggested a pre-Ordovician separation of what he considered the two most primitive tabulates, the lichenariids and the auloporids. Initially, Scrutton (1979) also favoured a pre-Ordovician separation of these two groups, but because the earliest records of auloporids are uncertain, he now considers *Lichenaria* the ancestral tabulate coral (Scrutton 1984). Flower (1961) and Flower and Duncan (1975) also regarded *Lichenaria* as ancestral to all tabulate corals and believed *Aulopora* evolved from the lichenariids through *Eofletcheria*. Many workers recognize *Lichenaria* as the ancestral tabulate coral (Flower 1961; Flower and Duncan 1975; Scrutton 1979), principally because *Lichenaria* is the only tabulate coral reported from strata of Early Ordovician age (but see Sokolov 1955, 1962, for possible occurrence of Early Ordovician *Aulopora*). In contrast to these authors, Laub (1984) considered most early occurrences of *Lichenaria* as doubtful and therefore questioned the pre-eminent role of *Lichenaria* in the early evolution of tabulate corals.

In contrast to *Lichenaria* as the ancestral tabulate coral, many authors consider *Aulopora* and/or its relatives ancestral (Sokolov 1955, 1962; Ivanovskii 1965; Bondarenko 1966). There are two lines of reasoning offered in support of this hypothesis. First, Sokolov (1962, p. 208) reported *Aulopora* from the Lower Ordovician of southern Siberia and the Baltic area, even though the specimens have never been figured. Second, its morphological characteristics and similarity to Cambrian tabulate-like organisms, such as *Protoaulopora*, suggest to some workers that it is a very primitive tabulate coral (Sokolov 1955). Tube diameters of around 0·1 mm, however, may indicate an unlikely relationship to the corals (Scrutton, pers. comm. 1988).

Hill (1981) provided the most recent classification for tabulate corals. She divided the Ordovician taxa into several orders. A comparison of her classification, and that presented in Scrutton (1984), with the results from the phylogenetic analyses are presented on page 760.

MATERIAL AND METHODS

Phylogenetic analysis

Several methods for determining polarity of character state transformations are available to phylogenetic analysis: the ontogenetic method (Nelson 1978; Nelson and Platnick 1981; Patterson 1982, 1983; Kluge 1985; de Queiroz 1985) the palaeontological method (Harper 1976; Szalay 1977 *a*, *b*, *c*; Gingerich and Schoeninger 1977; Gingerich 1979), biogeography (Nelson and Platnick 1981; Wiley 1981), the functional approach (Fisher 1982), and outgroup comparison (Lundberg 1972; Stevens 1980; Watrous and Wheeler 1981; Wiley 1981; Farris 1982; Maddison *et al.* 1984). Whereas the theoretical rationales for these methods are the subject of intense debate (e.g. Nelson 1978, 1985; Nelson and Platnick 1981; de Queiroz 1985), in practice, many workers use the methodology that will provide the maximum amount of information from their particular data set.

For palaeobiologists working with extinct taxa, each of these methodologies poses additional limitations that are either not experienced by neontologists, or are only slight inconveniences when extinct taxa are added to an analysis of living organisms. Quite often, preservation of ontogenetic sequences in the fossil record is insufficient for meaningful comparisons to be made. In addition, if critical taxa are not preserved, the ontogenetic method may give erroneous results (de Queiroz 1985).

The limitations of the palaeontological method are well known (Nelson and Platnick 1981; Patterson 1981) and also stem from the lack of control of missing taxa. Of course, the reliability of determining the relative timing of appearance of character states increases over longer intervals of geological time. The palaeontological method has been reduced to a special case of the outgroup method (de Queiroz 1985).

The outgroup method, used in the present paper, and the ontogenetic method are the most widely agreed upon methods. Development in early tabulate corals is poorly known and this precluded the use of the ontogenetic method in this study. I chose to ignore strictly stratigraphical and biogeographical data in my phylogenetic methodology so that palaeontological hypotheses already formulated could be compared with hypotheses based only on morphology. The only exception to this is the choice of an outgroup: scleractinian corals were excluded from outgroup analysis because both the tabulate and rugose corals appeared in the Lower Palaeozoic, whereas the scleractinian corals did not appear until the Middle Triassic (some 300 myr later).

In the analysis of the orgination of a clade, added assumptions imposed on primitive taxa may unnecessarily constrain plausible evolutionary pathways. Therefore, the criterion implemented for evaluating phylogenetic relationships was parsimony, specifically global parsimony (as defined by Maddison *et al.* 1984) in which both character state reversals and convergences are allowed. This methodology entails the least number of assumptions, as opposed to other parsimony methodologies such as the Dollo (only a single origination of a character state is permitted; Farris 1977) or Camin-Sokal (reversal from derived character state back to an ancestral one is prohibited; Camin and Sokal 1965). In a group as morphologically simple as the tabulate corals, character states may have evolved several times or may have reverted back to ancestral states many times early in their evolution. Thus, only global parsimony was used as the criterion for arriving at a suitable phylogeny.

I used the Phylogenetic Analysis Using Parsimony (PAUP) (Version 2.4.1) program written by David Swofford of the Illinois Natural History Survey. The PAUP subroutine MULPARS searches for multiple equally parsimonious trees through branch-swapping. Several preliminary runs through the program without the MULPARS option revealed close correspondence between the two optimization options, FARRIS and MINF. FARRIS and MINF are two methods of assigning character states to hypothetical taxonomic units (HTU) along the tree. FARRIS optimization is presented in Farris (1970). MINF optimization assigns character states to the hypothetical taxonomic units so that the f-value of Farris (1972) is minimized, but the HTUs may only take states observed in at least one of the taxa under study and the tree length must be minimal (Swofford 1985). Because FARRIS could give ambiguous results when the tree was rooted by an ancestor (e.g. *Lichenaria*) (Swofford 1985), MINF was utilized in the analyses presented in this paper.

PAUP provides a consistency index for both trees and individual characters. The consistency index of a tree is a measure of the consistency of a particular tree to a data set. It is the sum, over all the characters, of the *range* of each character divided by the tree length for all characters (Kluge and Farris 1969). The *range* of a character is equivalent to the minimum length of a tree computed for that character only (Swofford 1985). The consistency index for an individual character is the minimum tree length calculated based on that character divided by the actual tree length computed based on the character. Each equally parsimonious tree is topologically distinct, but possesses the same number of character state changes (= tree length) and the same consistency index.

In all analyses conducted using MULPARS the upper limit of 100 equally parsimonious trees was found. It was therefore necessary to find any common topologies contained within all the minimum length trees. I used the CONTREE program written by Swofford which accompanies PAUP to compute two types of consensus trees: the Adams (1972) consensus tree and the *strict* consensus tree of Rohlf (1982). The goal of a consensus tree is to represent only the information that is common to all of the equally parsimonious trees. In *strict* consensus trees (Rohlf 1982), only those groups that appear on every equally parsimonious cladogram appear on the tree. In Adams (1972) consensus trees, both groups that appear on every equally parsimonious cladogram and groups which are intersections of groups found in all the original trees will appear. Because the Adams (1972) consensus tree provided a more resolved phylogeny than the Rohlf (1982) *strict* consensus tree, and because the Adams (1972) trees may be more powerful in detecting agreement among trees (Carpenter 1987), I examined the Adams trees to trace character state transitions and to define groups within the ingroup. Because consensus trees may not account for the morphological data as well as any of the equally parsimonious trees (i.e. they are derived from fundamental cladograms as opposed to the original data, Miyamoto 1985; Carpenter 1987). I present the consensus trees only as a set of phylogenetic hypotheses which should undergo further testing, and not as the solution to the phylogeny of early Ordovician Tabulata. The Rohlf (1982) *strict* consensus trees computed are available upon request from the author.

TABLE 1. Character states and codes for tabulate coral characters used in the LICHGRPS and RUGSGRPS analyses

Character number	Character name	Character state	Code
1	Tabulae	Absent	0
		Present	1
2	Tabulae shape	Horizontal	0
		Sub-horizontal	1
		Infundibuliform	2
3	Colony architecture	Cerioid	0
		Phaceloid	1
		Conical/trochoid	2
		Cateniform	3
		Reptant	4
		Dendroid	5
		Coenosteoid	6
4	Wall thickness, (relative to corallite diameter)	Thin	0
		Thick	1
		Thin axially; thick at surface	2
5	Mural pores	Absent	0
		Present	1
		Pore canals	2
6	Septa	Absent	0
		Present	1
7	Microstructure	Non-trabeculate	0
		Trabeculate	1
8	Corallite shape	Polygonal	0
		Rounded	1
		Subquadrate	2
		Stellate	3
		Elliptical	4
9	Coenenchyme	Absent	0
		Present	1
10	Pore arrangement	Vertical rows	0
		Sparse	1
		Horizontal rows	2
11	Rows of spines	Absent	0
		Present	1
12	Longitudinally corrugated walls	Absent	0
		Present	1
13	Transversely crenulated walls	Absent	0
		Present	1
14	Columella	Absent	0
		Present	1
15	Orders of septa	One	0
		Two	1
16	Stereozone	Absent	0
		Present	1
17	Vertical tubuli	Absent	0
		Present	1
18	Diaphragms	Absent	0
		Present	1
19	Horizontal tubules	Absent	0
		Present	1

TABLE 1. (*cont.*)

Character number	Character name	Character state	Code
20	Corallum	Solitary	0
		Colonial	1
21	Fossula	Absent	0
		Present	1
22	Septal insertion	Random	0
		In quadrants	1
23	Pore location	Corner	0
		Wall	1
		Corner and wall	2

Ingroup

The ingroup includes only those thirty-seven Ordovician tabulate genera of Scrutton (1984, fig. 1) with an additional taxon for *Eofletcheria*, an early non-trabeculate form without septa and a later trabeculate form with septa. The problematic tetradiid group was not included in the analysis because their taxonomic placement has been questioned (e.g. Scrutton 1979, 1984). In addition, because their morphology is so poorly understood, many characters would be represented as missing data, producing unreliable results. In addition to the 38 ingroup taxa, 3 separate outgroup taxa were included.

Outgroups

The selection of an outgroup is based on finding the sister group that shares a most recent common ancestor with the ingroup (Wiley 1981). Two phylogenetic analyses were undertaken. In the first the most primitive Ordovician rugose corals are the outgroup (RUGSGRPS) and in the second *Lichenaria* is the ancestor (LICHGRPS).

I conducted a phylogenetic analysis (RUGSGRPS) using what many workers consider the three most primitive Ordovician rugose corals, *Hillophyllum*, *Lambeophyllum*, and *Primitophyllum* (Webby 1971; Sytova 1977; Scrutton 1979) as an outgroup. I also considered using *Cothonion*, quite possibly a Cambrian rugose coral, but it is too poorly known at present to be regarded as a true rugosan (Scrutton 1979; Hill 1981). Regardless of whether the Rugosa were derived from the Ordovician tabulate corals (Flower 1961; Sokolov 1962; Webby 1971; Flower and Duncan 1975) or the tabulate and rugose corals evolved from the same ancestral stock in the Ordovician (Weyer 1973; Sytova 1977) or a common ancestry existed among their soft bodied Cambrian precursors (Scrutton 1979, 1984), the Palaeozoic corals are closely related, and the primitive rugosans provide a logical choice for an outgroup.

Most phylogenetic reconstructions composed by evolutionary systematists have depicted a *Lichenaria* ancestor, from which all later taxa were derived. I conducted a second phylogenetic analysis (LICHGRPS) using *Lichenaria* as the ancestor to compare phylogenetic trees constructed by previous workers based on a lichenariid ancestor with those obtained from a phylogenetic analysis.

A third possible outgroup might have involved a number of tabulate-like organisms reported from Cambrian strata. These tabulatomorph corals have not been previously incorporated in phylogenetic analyses for two reasons: first, they occur nearly 70 myr earlier than the earliest accepted tabulate, and because of such a large time interval have caused workers to perceive their evolution as not closely tied with tabulate coral evolution; and second, their paucity and poor state of preservation have discouraged detailed morphometric analyses. Although most cases of Cambrian zoantharians are questionable (Hill 1981), further discoveries and detailed palaeobiological investigations of such genera as *Cambrotrypa* and *Protoanlopora* may lead to the substantiation of a Cambrian coral fauna (Scrutton 1979). I have not evaluated the phylogenetic position of Cambrian tabulatomorphs in this paper for the reasons discussed above, but acknowledge, with Scrutton (1984), that this remains a promising field for future phylogenetic research.

Characters and character states

Twenty characters were used in the LICHGRPS analysis and 23 characters were used in the RUGSGRPS analysis. Table 1 gives the characters, character states, and codes used in the phylogenetic analysis and the appendix gives the coded data matrix. Morphological character states were obtained from Flower (1961), Hill (1981), Pandolfi (1985), Scrutton (1979, 1984), Sokolov (1962), and original descriptions where necessary. Multistate characters are unordered in the analysis. All characters are weighted equally.

It is important to note the extreme influence of choice of characters and character states in the analysis. I chose the characters on the basis of their being reported in systematic descriptions of the taxa, and upon how well understood they are. For example, corallite increase and presence/absence of an axial plate, although well understood in many early taxa, are not sufficiently known or reported in the majority of the taxa under study here to include in the phylogenetic study.

When dealing with taxa at the generic level, different states for the same character can coexist among congeneric species; character states for taxa displaying polymorphism in a particular character were chosen to be those that were the most widely distributed throughout the congeneric species. Many character states were taken from the Treatise where some terms are overlapping; hence in the character tabulae shape, the character states 'slightly arched or saucered' and 'subhorizontal' and 'edges upturned slightly' are all distinguished from one another in the Treatise, but are here treated as the character state 'subhorizontal'. In addition, it is almost certainly true that some of the characters are not homologous. For example, the origin of wall pores may be distinct in the heliolitids versus the favositids, yet both taxa were scored according to presence or absence of 'mural pores'. In addition, all forms of tabulate septa may not be homologous (Scrutton, pers. comm. 1987), and it seems as if the homology of coenenchyme among early tabulates also must be assessed.

Finally, in the appendix there are question marks representing either missing data or inapplicable character. For example only taxa which are coenenchymate (character 9) may possess the characters 'vertical tubuli' (character 17) and 'diaphragms' (character 18). Therefore, to avoid an unnecessarily weighted analysis (by virtue of coenenchyme being represented by three characters instead of one) and for the coenenchyme characters to be applicable to only the coenenchymate taxa, question marks are used for characters 17 and 18 for non-coenenchymate bearing taxa. A similar situation arises with mural pores (characters 5, 10 and 23) and septa (characters 6, 11, 15 and 22).

RESULTS

The two phylogenetic analyses were each run both with and without MULPARS. Table 2 gives the tree lengths and consistency indices for these two analyses and for a tree whose topology is consistent with that presented by Scrutton (1984, text-fig. 1, p. 113). In the results presented below, a Wagner neighbourhood refers to three taxa joined together at a single node, two of which are more closely related to each other than either is to the third (Brooks 1984).

Primitive rugosans as outgroup (RUGSGRPS)

In an analysis undertaken with MULPARS, at least 100 equally parsimonious trees were found, each having a tree length of 81 and a consistency index of 0·444 (Table 2). A consensus tree based on the 100 trees was obtained using CONTREE. In the Adams consensus tree (text-fig. 1), four major groupings within the ingroup can be differentiated. These are: Group I – the auloporids, early *Eofletcheria*, and the halysitids (text-fig. 2), Group II – *Adaverina* and forms with horizontal connections between modules (corallites) (text-fig. 2), Group III – cerioid colonies with polygonal corallites, with or without mural pores (text-fig. 3) and Group IV – coenenchymate taxa (text-fig. 4). All groups are unresolved with respect to each other and with respect to *Reuschia*, later *Eofletcheria*, *Kolymopora* and *Tollina* (text-fig. 1).

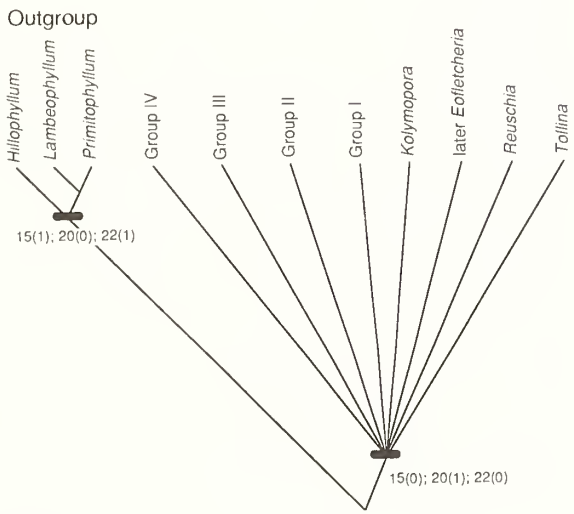
Lichenaria as outgroup (LICHGRPS)

In an analysis undertaken with MULPARS, at least 100 equally parsimonious trees were found, each having a tree length of 72 and consistency index of 0·431 (Table 2). A consensus tree based on the 100 trees was obtained using CONTREE. In the Adams consensus tree (text-fig. 5), five major groupings within the ingroup can be differentiated. These are: Group A – *Saffordophyllum*, *Manipora*, and cerioid thin-walled taxa with or without mural pores (text-fig. 6); Group B – thick-walled taxa lacking mural pores (text-fig. 7); Group C – the auloporids, early *Eofletcheria*, and the

TABLE 2. Tree lengths and consistency indices for LICHGRPS, RUGSGRPS, and tree proposed in Scrutton (1984). Identical values were obtained with and without MULPARS

Root	Tree length	Consistency index
Lichenaria (ancestor)	72	0·431
Primitive Ordovician rugosans (outgroup)	81	0·444
Scrutton (1984) topology	96	0·323

halysitids (text-fig. 2); Group D – *Adaverina* and forms with horizontal connections between corallites (text-fig. 2) and Group E – coenenchymate taxa (text-fig. 4).



TEXT-FIG. 1. Adams (1972) consensus tree for RUGSGRPS phylogenetic analysis. Groups I–IV are shown in text-figs. 2–4. The outgroup includes the Ordovician rugose coral genera *Primitophyllum*, *Lambeophyllum*, and *Hillophyllum*. See Table 1 for character states and codes.

DISCUSSION

The goal of the phylogenetic analyses presented here is threefold: 1, to compare existing phylogenies to an analysis based on cladistic methodology, 2, to determine the homology of morphological characters of tabulate corals by evaluating patterns of character consistency among the early tabulate corals, and 3, to compare the phylogenetic analysis with current classification schemes of the Tabulata.

Phylogenetic analysis

RUGSGRPS analysis. Group I is a trichotomy which includes the aporous, aseptate auloporids, the aporous cateniform halysitids, and early *Eofletcheria* (text-fig. 2). Auloporids have been suggested by some workers to be ancestral to all tabulate corals, primarily because of the presence of *Protoaulopora* in the Cambrian (e.g. Sokolov 1955, 1962; Bondarenko 1966). However, most western workers have not placed much confidence in drawing phylogenies based on Cambrian occurrences of tabulate-like animals and have envisaged auloporids descending through *Eofletcheria* (Hill 1953; Flower 1961; Flower and Duncan 1975; Scrutton 1984). The phylogenetic analysis presented here does not falsify a close phylogenetic relationship between the auloporids and *Eofletcheria*.

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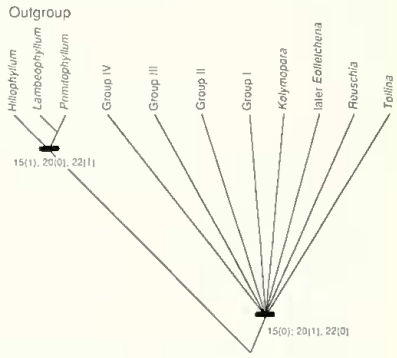

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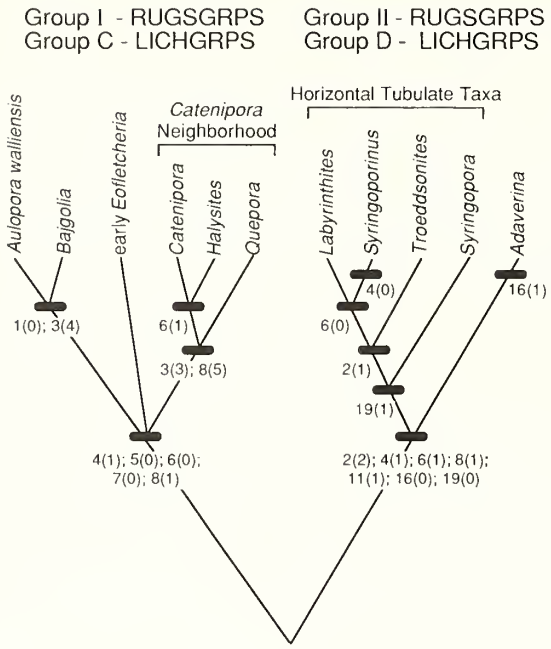


TEXT-FIG. 2. Adams (1972) consensus tree of Group I and Group II in the RUGSGRPS analysis and Groups C and D in the LICHGRPS analysis. Groups I and C consist of the halysitids with cateniform colony architecture, and members of the Auloporida (*sensu* Hill 1981). Groups II and D consist of the horizontal tubulate taxa and the aulocystid *Adaverina*. Note that Groups I and II and all other groups in the RUGSGRPS analysis are unresolved with respect to one another. They are shown together here for brevity's sake. See Table 1 for character states and codes.

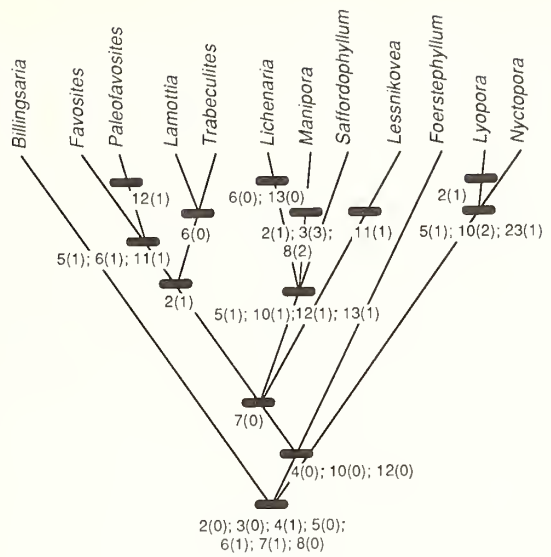
The *Catenipora* Wagner neighbourhood is resolved because *Halysites* and *Catenipora* both possess septa, whereas *Quepora* does not. The evolution of *Catenipora* from *Quepora*, proposed by numerous workers (Flower 1961; Flower and Duncan 1975; Scrutton 1984), is not falsified by the cladogram (test-fig. 2).

Group II is composed of *Adaverina*, and the taxa with horizontal connecting tubes (test-fig. 2). These aporous, non-cerioid taxa possess septa in rows and all except *Adaverina* possess horizontal tubes and lack a stereozone (text-fig. 2). *Labyrinthites* and *Syringoporinus* are united by virtue of lacking septa, *Troedssonites* forms a sister group to these 2 taxa by virtue of sub-horizontal tabulae, and *Syringopora* forms a sister group to these three taxa by virtue of possessing horizontal tubes (text-fig. 2).

Relationships within cerioid taxa with polygonal corallites comprising Group III can be resolved by wall thickness and curvature, septa, and development of mural pores (text-fig. 3). The unresolved trichotomy composed of *Lichenaria*, *Saffordophyllum*, and *Manipora* is based on their possession of sparse mural pores and longitudinal wall corrugations. The close phylogenetic association of these three taxa is agreed upon by most workers (Flower 1961; Flower and Duncan 1975; Scrutton 1979, 1984) and is not falsified by the RUGSGRPS phylogenetic analysis. *Favosites* and *Paleofavosites* share a common ancestry on the basis of the synapomorphies mural pores in vertical rows, rows of septal spines, and horizontal tabulae. The notion that *Saffordophyllum* is ancestral to the favositids (Scrutton 1984) is not falsified by the phylogenetic analysis because the *Lichenaria* trichotomy is unresolved with respect to the *Paleofavosites/Favosites* and *Lamottia/Trabeculites* branches (text-fig. 3).

Paleofavosites and *Favosites*, along with *Lessnikovea*, are the only taxa in Group III that have septa in rows. The trichotomy represented by the *Lichenaria* trichotomy, *Lessnikovea*, and the *Paleofavosites/Favosites* and *Lamottia/Trabeculites* branch is derived with respect to *Foerstephyllum* (text-fig. 3). Flower (1961) and Flower and Duncan (1975) believed *Foerstephyllum* to be of primary importance in the later evolution of tabulate and perhaps rugose corals.

Closely associated with these thin-walled cerioid taxa are the thick-walled, septate, cerioid *Billingsaria*, *Lyopora*, and *Nyctopora*. *Lyopora* has been suggested to have evolved from *Billingsaria* (Scrutton 1984) but in the RUGSGRPS phylogenetic analysis. *Lyopora* seems to be more closely



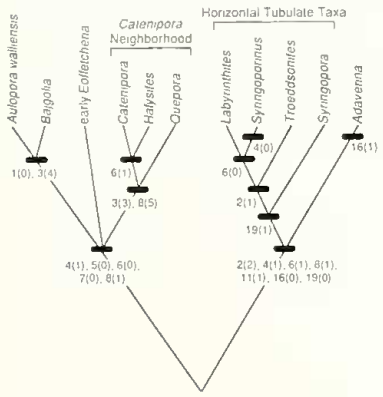
TEXT-FIG. 3. Adams (1972) consensus tree of Group III in the RUGSGRPS phylogenetic analysis. Group III is represented by taxa with a cerioid colony architecture, thin- or thick-walled, with the mural pore-bearing taxa derived with respect to the aporous taxa. See Table 1 for character states and codes.

related to *Nyctopora* than either is to *Billingsaria* (text-fig. 3). Contrary to Scrutton (1984), *Eofletcheria* does not appear to be associated with these thick-walled taxa.

Group IV is united by the character coenenchyme. The relationships within Group IV are unique to the present analysis and are preliminary because many of the apomorphic characters of coenenchymate taxa were not included in the analysis. For example, Webby and Kruse (1984) provided morphological data on the various types of coenenchyme which suggested to them that *Coccoseris* gave rise to *Heliolites* which in turn gave rise to *Propora* and *Plasmoporella*. However, text-fig. 4 shows *Coccoseris* to be more closely related to *Plasmoporella* than either is to either *Heliolites* or *Propora*. More data are needed to evaluate Webby and Kruse's (1984) claims. The stratigraphical evidence offered by Webby and Kruse (1984) should be corroborated by other sections.

Morphological characters useful in differentiating coenenchymate taxa were tabulae, columella, mural pores, and diaphragms (text-fix. 4). Within Group IV a polychotomy exists between *Propora*, *Heliolites*, and the rest of the coenenchymate taxa. These latter taxa are highly resolved into two sister groups (text-fix. 4). One group possesses mural pores (with the exception of *Sarcinula*, which possesses pore canals) and the other possesses either a columella or no tabulae (text-fig. 4). The presence of *Sarcinula* with the heliolitids is perhaps surprising and the character, coenenchyme may not be homologous between this taxon and the other coenenchymate taxa.

Flower (1961), Flower and Duncan (1975), and Scrutton (1984) identified *Nyctopora* as a logical precursor to *Calapoecia*, and hence the coenenchymate taxa. Scrutton (1984) noted in *N. goldfussi* the presence of juvenile offsets which have retarded development with respect to other taxa. In other species of *Nyctopora* offsets are generally small and have closely spaced tabulae for a very short length, and quickly develop into adults with large diameters and moderately spaced tabulae. In *N. goldfussi* however, offsets retain their small size and closely spaced tabulae for up to 4 or 5 times the length of offsets of other species of *Nyctopora* before eventually developing into large adult corallites with moderately spaced tabulae (Scrutton 1984). Coenenchyme may therefore have developed due to heterochronic retardation in the development of juvenile offsets such that the offsets retained the juvenile morphology into adulthood (Pandolfi 1988) (text-fig. 8). Although Scrutton (1984) discounted the possibility of *N. goldfussi* as ancestral to *Calapoecia* based on current knowledge of fossil occurrences, a hypothesis of heterochrony is not falsified by the RUGSGRPS phylogenetic analysis (text-figs. 1, 3, 4). Heterochrony occurs elsewhere in the early tabulate corals, but its role in tabulate coral evolution is in need of further study (Pandolfi 1984, 1988).



TEXT-FIG. 2. Adams (1972) consensus tree of Group I and Group II in the RUGSGRPS analysis and Groups C and D in the LICHGRPS analysis. Groups I and C consist of the halysitids with cateniform colony architecture, and members of the Auloporida (*sensu* Hill 1981). Groups II and D consist of the horizontal tubulate taxa and the aulocystid *Adaverina*. Note that Groups I and II and all other groups in the RUGSGRPS analysis are unresolved with respect to one another. They are shown together here for brevity's sake. See Table 1 for character states and codes.

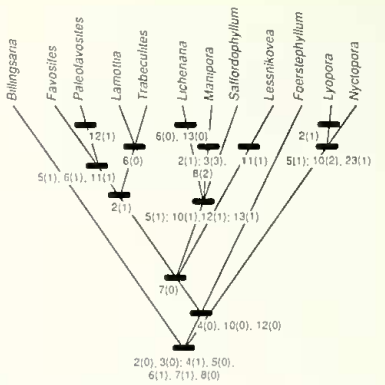
The *Catenipora* Wagner neighbourhood is resolved because *Halysites* and *Catenipora* both possess septa, whereas *Quepora* does not. The evolution of *Catenipora* from *Quepora*, proposed by numerous workers (Flower 1961; Flower and Duncan 1975; Scrutton 1984), is not falsified by the cladogram (test-fig. 2).

Group II is composed of *Adaverina*, and the taxa with horizontal connecting tubes (test-fig. 2). These aporous, non-cerioid taxa possess septa in rows and all except *Adaverina* possess horizontal tubes and lack a stereozone (text-fig. 2). *Labyrinthites* and *Syringoporinus* are united by virtue of lacking septa. *Troedssonites* forms a sister group to these 2 taxa by virtue of sub-horizontal tabulae, and *Syringopora* forms a sister group to these three taxa by virtue of possessing horizontal tubes (text-fig. 2).

Relationships within cerioid taxa with polygonal corallites comprising Group III can be resolved by wall thickness and curvature, septa, and development of mural pores (text-fig. 3). The unresolved trichotomy composed of *Lichenaria*, *Saffordophyllum*, and *Manipora* is based on their possession of sparse mural pores and longitudinal wall corrugations. The close phylogenetic association of these three taxa is agreed upon by most workers (Flower 1961; Flower and Duncan 1975; Scrutton 1979, 1984) and is not falsified by the RUGSGRPS phylogenetic analysis. *Favosites* and *Paleofavosites* share a common ancestry on the basis of the synapomorphies mural pores in vertical rows, rows of septal spines, and horizontal tabulae. The notion that *Saffordophyllum* is ancestral to the favositids (Scrutton 1984) is not falsified by the phylogenetic analysis because the *Lichenaria* trichotomy is unresolved with respect to the *Paleofavosites*/*Favosites* and *Lamottia*/*Trabeculites* branches (text-fig. 3).

Paleofavosites and *Favosites*, along with *Lessnikovea*, are the only taxa in Group III that have septa in rows. The trichotomy represented by the *Lichenaria* trichotomy, *Lessnikovea*, and the *Paleofavosites*/*Favosites* and *Lamottia*/*Trabeculites* branch is derived with respect to *Foerstephyllum* (text-fig. 3). Flower (1961) and Flower and Duncan (1975) believed *Foerstephyllum* to be of primary importance in the later evolution of tabulate and perhaps rugose corals.

Closely associated with these thin-walled cerioid taxa are the thick-walled, septate, cerioid *Billingsaria*, *Lyopora*, and *Nyctopora*. *Lyopora* has been suggested to have evolved from *Billingsaria* (Scrutton 1984) but in the RUGSGRPS phylogenetic analysis, *Lyopora* seems to be more closely



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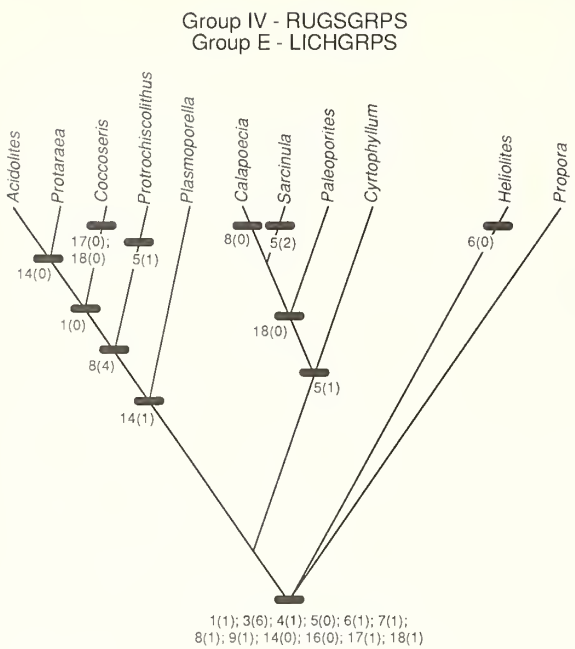
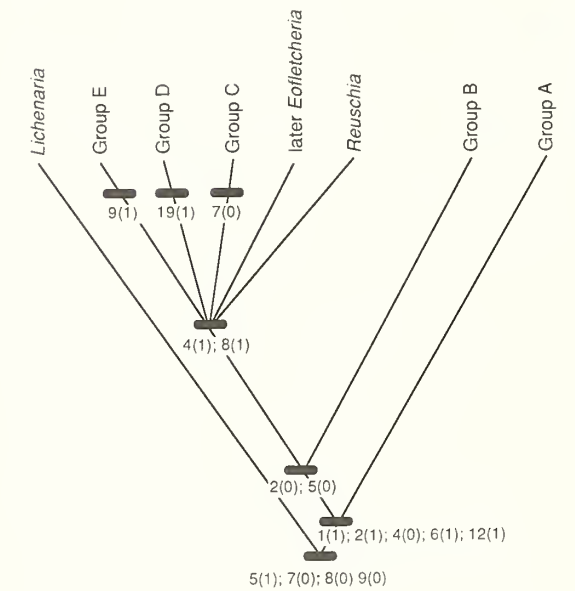


TEXT-FIG. 4. Adams (1972) consensus tree of Group IV in the RUGSGRPS analysis and Group E in the LICHGRPS analysis. This Group is represented by taxa possessing coenenchyme. See Table 1 for character states and codes.



TEXT-FIG. 5. Adams (1972) consensus tree obtained in the LICHGRPS phylogenetic analysis. Groups A–E are shown in text-figs. 2, 4, 6–8. The analysis was undertaken with the tree rooted with *Lichenaria* as the ancestral tabulate coral. See Table 1 for character states and codes.

LICHGRPS analysis. Group A is composed of a trichotomy involving the sparsely porous *Manipora* and *Saffordophyllum* and the cerioid thin-walled taxa with mural pores (text-fig. 6). *Manipora* and *Saffordophyllum* possess transversely crenulated walls (text-fig. 6). Most workers believe these two genera to be closely associated with *Lichenaria* (Flower 1961; Flower and Duncan 1975; Scrutton 1979, 1984) and the LICHGRPS analysis corroborates this claim.

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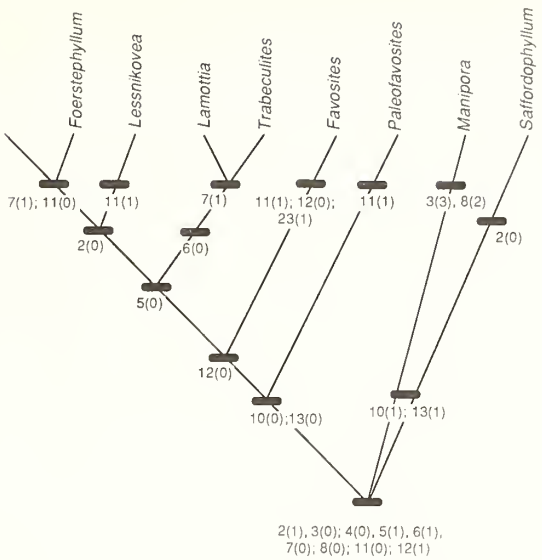


TEXT-FIG. 6. Adams (1972) consensus tree of Group A in the LICHGRPS phylogenetic analysis. Both *Manipora* and *Saffordophyllum* have sparse mural pores and transversely crenulate walls, and are unresolved with respect to one another and to cerioid thin-walled taxa possessing mural pores. Included here as derived are taxa typically regarded as members of the Sarcinulida. See Table 1 for character states and codes.

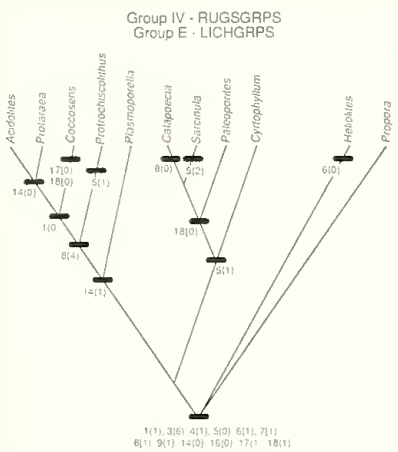
it is not unlikely for *Trabeculites* to have been derived from porous predecessors (Flower and Duncan 1975). As in Group B, Group A contains taxa which have been regarded as Sarcinulida: *Lamottia* (Scrutton 1984) and *Lessnikovea* (Hill 1981). The position of Group A on the LICHGRPS cladogram suggests that these two taxa may represent relatively primitive members of the Sarcinulida clade.

Group B is apparently a morphologically assorted group of thick-walled taxa which includes the aporous taxa *Billingsaria*, *Nyctopora*, *Lyopora*, and *Tollina* and the porous taxon *Kolymopora* (text-fig. 7). This group contains three taxa from the Sarcinulida clade proposed by Scrutton (1984, text-fig 1, p. 113) for the radiation of the Ordovician Tabulata. *Tollina* and *Kolymopora*, however, are shown in disparate sections of Scrutton's (1984) phylogeny, Lichenariida for the former and Favositida for the latter.

Groups C, D and E are identical to Groups I, II and IV respectively, in the RUGSGRPS analysis but are unresolved with respect to *Reuschia*, which possesses a stereozone, and later *Eofletcheria* (text-fig. 5). Several authors have depicted a close phylogenetic association between *Aulopora*, *Eofletcheria*, and *Reuschia* (Flower and Duncan 1975; Scrutton 1984). Scrutton discussed the possible phylogenetic association of *Adaverina* and *Reuschia* with *Eofletcheria* and the auloporids. He envisioned *Reuschia* evolving directly from *Eofletcheria*, whereas *Adaverina* evolved from *Eofletcheria* through an intermediary, *Aulopora*. The LICHGRPS analysis shows that these groups share a common ancestry, but relationships between the groups are unresolved (test-figs. 2 and 5).

Group E is the same as Group IV of the RUGSGRPS analysis and is united by the presence of coenenchyme (text-fig. 4). Again *Nyctopora* is less derived than *Calapoecia* (text-figs. 4 and 7) and the hypothesis that coenenchyme evolved through *N. goldfussi* by heterochrony is not falsified by the LICHGRPS phylogenetic analysis.

Comparison between analyses. Several differences exist between the Adams (1972) consensus trees produced from the two analyses. The first eight taxa of the LICHGRPS analysis are members of Group III in the RUGSGRPS analysis (text-figs. 3 and 6). The relationships between these taxa are slightly better resolved with the LICHGRPS analysis than the RUGSGRPS analysis. In the RUGSGRPS analysis, *Lichenaria* is a derived taxon and plays a relatively minor role in the diversification of the Ordovician tabulates (text-fig. 3). In the LICHGRPS analysis *Foerstephyllum* appears early in the tree and may have given rise to more derived groups (Flower 1961; Flower and Duncan 1975).



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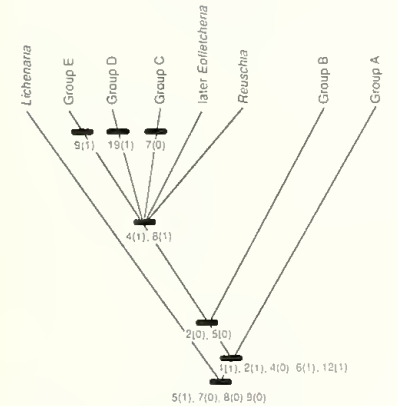

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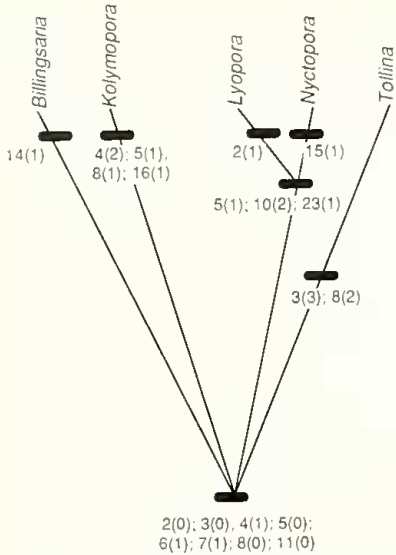

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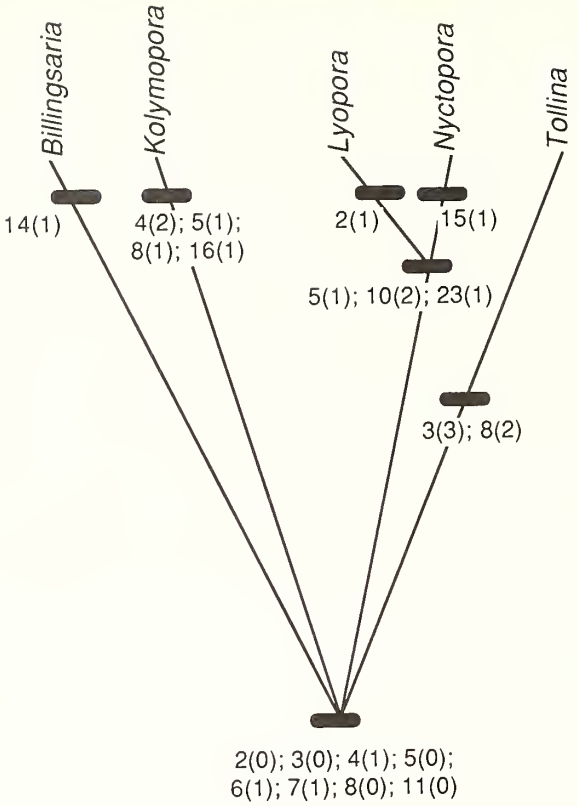
The cateniform and auloporid taxa are identically resolved in the two analyses. In the LICHGRPS analysis they occur as relatively derived Group C unresolved with the horizontally tubulate taxa and the coenenchymate taxa (text-fig. 5). This is in marked contrast with the RUGSGRPS analysis in which the cateniform and auloporid taxa appear as Group 1, unresolved with respect to all other groups (text-fig. 1). Finally, the coenenchymate clades are identical between the two analyses; however, in the LICHGRPS analysis the group is relatively derived and only unresolved with respect to the horizontal tubulate taxa and the auloporid/halysitid taxa (text-fig. 5), whereas in the RUGSGRPS analysis it is unresolved with respect to all other groups (text-fig. 1).

The LICHGRPS analysis yielded groups somewhat different from the RUGSGRPS analysis, but neither produced results completely consistent with previously proposed phylogenies. Table 2 shows that whereas the LICHGRPS analysis yielded a lower tree length (72), and, ostensibly, a more parsimonious tree, than the RUGSGRPS analysis (81), the latter yielded a higher consistency index, indicating fewer character state transitions. One might expect a lower tree length for a tree rooted by a member of the ingroup than for one rooted by an outgroup. Meacham (1984) explained that a directed analysis which is rooted with any member of the ingroup will give the same results as those produced with an undirected analysis, or one which is performed on an unrooted tree. The extra taxa and characters utilized in the directed analysis, that is with the rugose outgroup, were responsible for six additional evolutionary steps that could not have occurred in the LICHGRPS analysis due to its undirected nature. Therefore, a more reasonable comparison would be a difference in tree length of three steps.

In a parsimony analysis, it is not immediately clear, based on tree length and CI, which tree is preferable. I present these two analyses impartially to provide a preliminary working hypothesis of relationships with which to compare further phylogenetic studies of tabulate corals. It seems clear



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